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LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *TRUPANEA SIGNATA* FOOTE (DIPTERA: TEPHRITIDAE) ON *GNAPHALIUM LUTEO-ALBUM* L. IN SOUTHERN CALIFORNIA

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Abstract.—*Trupanea signata* L. is a narrowly oligophagous, multivoltine, gregarious, obligately gallicolous fruit fly (Diptera: Tephritidae) studied in southern California on *Gnaphalium luteo-album* L. This host plant is an introduced weedy annual of Old World origin to which this tephritid has transferred from indigenous, congeneric hosts, an uncommon occurrence among nonfrugivorous North American Tephritidae. The egg, third-instar larva, and puparium are described and figured. The eggs are inserted into apical and axillary buds. From one to six larvae feed gregariously within an open cavity in the expanded pith parenchyma of galls on axillary branches and stems during all three instars. The galls are elongate-obclavoidal, sometimes bear axillary branches and flower heads, and are covered by a wooly investiture. Pupariation occurs inside the gall. The adults emerge and exit the gall through a common channel by pushing aside a thin, pre-formed, apical, "gall cap." The adults are long-lived and are the overwintering stage. The life cycle follows the aggregative pattern and at least two generations, one each in spring and fall, are produced annually on *G. luteo-album.* Two species of solitary, larval-pupal, hymenopterous endoparasitoids are reported: *Eurytoma* sp. (Eurytomidae) and *Pteromalus* sp. (Pteromalidae).

Key Words: Insecta, *Trupanea, Gnaphalium,* biology, taxonomy of immature stages, galls, oligophagy, parasitoids

The genus *Trupanea* (Diptera: Tephritidae) occurs worldwide and is a numerically large and widespread taxon of nonfrugivorous fruit flies in North America and California (Foote and Blanc 1963, Foote et al. 1993). As such, the adults are among the most commonly encountered, reared or swept tephritids; however, the life histories of most species remain little known, and several species are difficult to distinguish morphologically (Foote 1960, Foote et al. 1993). Detailed life histories of five species of *Trupanea* from southern California have been published (Cavender and Goeden 1982, Goeden 1987, 1988, Headrick and Goeden 1991, Knio et al. 1996b), and the immature stages of three of these species also described (Cavender and Goeden 1982, Headrick and Goeden 1991, Knio et al. 1996a). This and our next five papers will more than double the number of species of *Trupanea* for which life histories and immature stages are well known, beginning here with the indigenous, obligate gall-former, *T. signata* Foote.

MATERIALS AND METHODS

Our field studies on *T. signata* mainly focused on laboratory dissections of galls collected on *Gnaphalium luteo-album* L. at different locations in central and southern California during 1989–91: (1) N end of

Hemet Lake at 1424-m elevation, San Bernardino Nat. Forest (S section), Riverside Co., 29.ix.1989 and 11.ix.1990; (2) along Deer Creek in the Morton Flat area at 550 m. Tulare Co., 14.vi.1990; (3) Box Springs Grade between Moreno Valley and Riverside at 470 m, Riverside Co., 20–28.ii.1991. Excised galls and uprooted gall-bearing shoots were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Fifteen eggs recovered from ovipositional cagings and two second- and eight third-instar larvae, and four puparia dissected from galls were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in Hexamethlydisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for longevity studies, and those with the wicks wrapped around root-bearing shoots of *G. luteo-albun* for oviposition studies, in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod. Virgin male and female flies obtained from emergence vials were paired (n = 16) in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1991, 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Munz (1974, as updated by Hickman 1993); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Knio et al. (1996a) and Goeden and Teerink (1996a, b, c, 1997a, b) and our earlier works cited therein. Means ± SE are used throughout this paper. Voucher specimens of *T. signata* and its parasitoids reside in the research collections of RDG; preserved specimens of eggs, larvae and puparia are stored in a separate collection of immature Tephritidae maintained by JAT.

Results and Discussion

Taxonomy

Adult.—*Trupanea signata* was described from reared and swept adults collected from various locations in California by Foote (1960), who also pictured the wing of a female. Foote et al. (1993) illustrated the head of an adult in side view and the wing pattern of a female, and noted that the wing pattern of the male ". . .does not differ from that of the female in any important respect."

Immature stages.—*Egg*: Twenty-one eggs of *T. signata* were white, opaque, smooth; with an elongate-ellipsoidal body, 0.69 ± 0.005 (range, 0.65–0.74) mm long, 0.21 ± 0.004 (range, 0.17–0.23) mm wide, smoothly rounded at tapered posterior end, and with a peg-like anterior pedicel, 0.02 mm long (Fig. 1); a single row of aeropyles circumscribes the pedicel (Fig. 1).

The egg of *T. signata* is similar in shape to the eggs of other *Trupanea* species previously described. The egg is larger in width and length than *T. californica* Malloch, approximately the same size as *T. imperfecta* (Coquillett), and shorter than *T. conjuncta* (Adams), *T. bisetosa* (Coquillett) and *T. nigricornis* (Coquillett) (Goeden

Fig. 1. Egg of *Trupanea signata:* pedicel with aeropyles.

1987, 1988; Headrick and Goeden 1991; Knio et al. 1996a). The single row of aeropyles circumscribing the pedicel is similar to *T. nigricornis,* whereas, *T. bisetosa* commonly has two rows of aeropyles (Knio et al. 1996a).

Third instar: White, barrel-shaped, tapering anteriorly, rounded posteriorly; minute acanthae circumscribe each thoracic and abdominal segment anteriorly, gnathocephalon conical (Fig. 2A), rugose pads dorsally and laterally, rugose pads laterad of mouth lumen serrated on ventral margin (Fig. 2A-1); dorsal sensory organ consists of a single dome-shaped papilla (Fig. 2A-2, B-1); anterior sensory lobe bears four sensory organs, lateral sensory organ with a distinct central papilla (Fig. 2B-2); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 2B-3); mouth hooks tridentate; rugose pads circumscribe prothorax posteriorly of minute acanthae (Fig. 2C-1), single row of verruciform sensilla circumscribe prothorax medially (Fig. 2C-2); anterior thoracic spiracles on posterior margin of prothorax, bear 4–5 rounded papillae (Fig. 2C-3, 2D); metathoracic lateral spiracular complex consists of a spiracle and a single verruciform sensillum; abdominal lateral spiracular complex consists of a spiracle (Fig. 2E-1), a verruciform sensillum (Fig. 2E-2), and placoid-type sensillum (Fig. 2E-3); caudal segment smooth medially, circumscribed anteriorly by minute acanthae (Fig. 2F-1); posterior spiracular plates (Fig. 2F-2), with three ovoid rimae, ca. 0.038 mm in length (Fig. 2G-1), and four interspiracular processes each with 3–6 branches, longest measuring 0.013 mm (Fig. 2G-2); intermediate sensory complex ventrad of posterior spiracular plates among the minute acanthae (Fig. 2F-3), consist of a medusoid sensillum (Fig. 2H-1), and a stelex sensillum (Fig. 2H-2).

Trupanea signata is similar in general appearance to other described species, i.e., *Trupanea californica* (Headrick and Goeden 1991), *T. bisetosa* and *T. nigricornis* (Knio et al. 1996a). The anterior portion of the prothorax is circumscribed by minute acanthae and rugose pads, which appear to be characteristic of the genus *Trupanea* (Headrick and Goeden 1991, Knio et al. 1996a). Differences among *Trupanea* species described to date are found in the abdominal lateral spiracular complex. This complex in *T. californica* includes a single verruciform sensillum; in *T. nigricornis,* two verruciform sensilla; and in *T. bisetosa,* two verruciform sensilla and a placoid type sensillum (Headrick and Goeden 1991, Knio et al. 1996a). *Trupanea signata* also differs slightly in the number of branches in the interspiracular processes; *T. californica* and *T. bisetosa* possess 6–8 branches, *T. nigricornis* is similar to *T. signata* in having 3–6 branches (Headrick and Goeden 1991, Knio et al. 1996a).

Puparium: Puparium of *T. signata* shiny black, elongate-ellipsoidal, anterior end bears the invagination scar (Fig. 3A-1), and anterior thoracic spiracles (Fig. 3A-2), caudal segment bears the posterior spiracular plates (Fig. 3B-1), a band of minute acanthae (Fig. 3B-2), and the intermediate sensory complex (Fig. 3B-3). Forty-four puparia of *T. signata* averaged 3.23 ± 0.04 (range, 2.55–3.80) mm in length; 1.48 ± 0.03 (range, 1.10–2.35) mm in width.

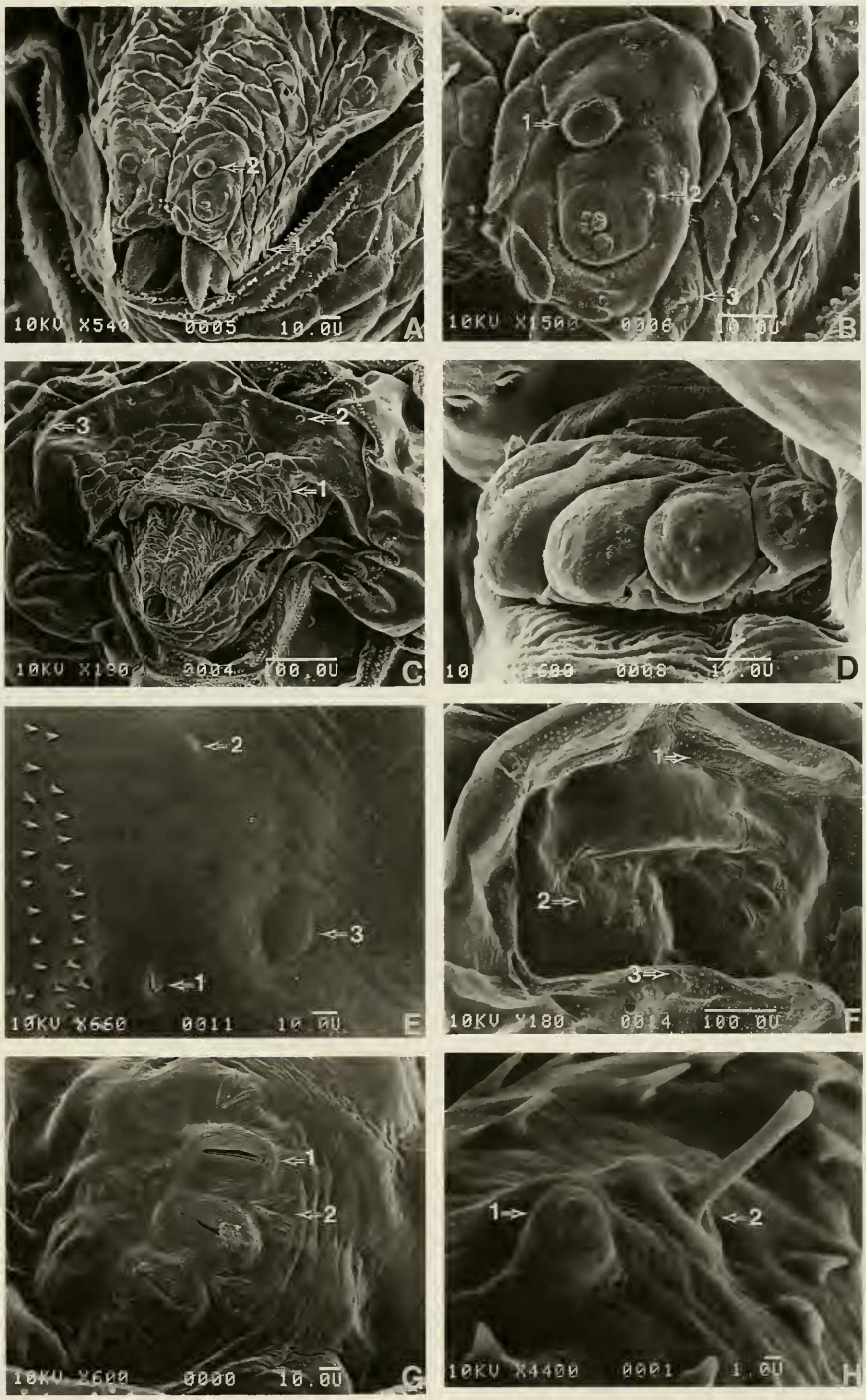

Fig. 2. Third instar of *Trupanea signata:* (A) gnathocephalon, anterior view, 1—serrated rugose pads, 2—dorsal sensory organ; (B) anterior sensory lobe, 1—dorsal sensory organ, 2—lateral sensory organ, 3—stomal sense organ; (C) anterior view, 1—prothoracic rugose pads, 2—verruciform sensilla, 3—anterior thoracic spiracle; (D) anterior thoracic spiracle; (E) fourth abdominal segment, lateral spiracular complex, 1—spiracle, 2—verruciform sensillum, 3—placoid-type sensillum; (F) caudal segment, 1—minute acanthae, 2—posterior spiracular plate, 3—intermediate sensory complex; (G) posterior spiracular plate, 1—rima, 2—interspiracular process; (H) intermediate sensory complex, 1—medusoid sensillum, 2—stelex sensillum.

Fig. 3. Puparium of *Trupanea signata:* (A) anterior end, 1—invagination scar, 2—anterior thoracic spiracles; (B) caudal segment, 1—posterior spiracular plate, 2—minute acanthae, 3—intermediate sensory complex.

Distribution and Hosts

The distribution of *T. signata* mapped by Foote et al. (1993) included the western U.S. north of Mexico and Canada, with this species recorded from Arizona, California, Colorado, Nebraska, New Mexico, Oregon, Texas, and Washington as well as British Columbia. Foote (1960) and Foote et al. (1993) reported *Anaphalis* sp. and *Gnaphalium stramineum* Kunth as hosts, besides *G. luteo-album* reported by Goeden (1992). *Gnaphalium luteo-album* is an introduced annual plant species of Old World origins (Munz 1974). Thus, *T. signata* like *T. californica* (Headrick and Goeden 1991), provide examples of indigenous, oligophagous tephritids that have adopted this non-indigenous, host-plant species that is congeneric with native hosts in the southern California flora (Munz 1974). Besides *Campiglossa genalis* (Thomson) on *Senecio* spp. (Goeden et al. 1994), few other examples of such host-plant transfer by indigenous, oligophagous, nonfrugivorous Tephritidae have been documented (Goeden 1996). The biological significance of the sweep record for a female of *T. signata* reported by Goeden (1986) and Foote et al. (1993) was its location on Santa Cruz Island, not the nonhost, *Baccharis pilularis* de Candolle from which it was swept, which like all-too-many sweep records for adult, nonfrugivorous Tephritidae are poor and often misleading indicators of reproductive-host-plant affinities. Accordingly, *T. signata* is oligophagous on certain species of *Anaphalis* and *Gnaphalium* of the subtribes Cassiniinae and Gnaphaliinae, respectively, and the tribe Gnaphalieae of the Asteraceae (Bremer 1994). Unlike *T. conjuncta, T. signata* apparently is an obligate, not a facultative gall former, and has not been reared from flower heads of *Anaphalis* or *Gnaphalium* spp. (Foote 1960, Foote et al. 1993, Goeden 1983, 1987, 1992, unpublished data). Also, our study sites 1 and 2 were in grazed, disturbed, riparian areas and site 3 was in a regularly and well irrigated, roadside flower bed, so all galled plants were well-watered.

Biology

Egg.—Eggs were inserted pedicel-last, singly or side-by-side, in small clusters of two to four for ca. two-thirds their lengths in terminal buds of stems or upper axillary branches (Fig. 4A). Unlike *T. conjuncta,* which also forms galls, the egg clusters were not glued together posteriorly (Goeden 1987).

Larva.—Newly-hatched first instars tunnelled basipetally into the pith of the stem or axillary branch to which they confine their feeding (Fig. 4B–D). The larvae feed singly or gregariously in open, elongate central cavities on proliferating pith paren-

Fig. 4. Life stages of *Trupanea signata* on *Gnaphalium luteo-album*: (A) pair of eggs (arrow) inserted in axillary bud, (B) third instar in feeding cavity below partially dislocated gall cap, (C) exterior view of apical bud gall, (D) gall of axillary branch with flower head at apex, (E) Four puparia in common feeding cavity below apical exit channel and gall cap. (F) Female adult at rest. Lines = 1 mm.

chyma (callose tissue), shallowly pitting the walls, and continually expanding the lengths and widths of the cavities during all three stadia (Fig. 4D). The gall cavities remained free of frass and solid waste, except for the discarded cephalopharyngeal skeletons of the first and second instars. The fully grown third instar extends the cavity distally by eating out a 5.2 ± 0.3 (range, 2–8) mm-long, exit tunnel (n = 25) through the shoot tip to just beneath the apex, leaving a hollow, tomentum-covered gall "cap," which it coats inside with voided liquid feces. The feces dry, harden, and hold this cap in place during pupariation (Fig. 4D). The larva then returns to the main gall cavity, where it and other mature larvae within pupariate with their heads facing the gall apex.

Pupa.—One hundred thirteen full-sized galls collected at all three study sites each contained an average of 2 ± 1 (range, 1–6) puparia (Fig. 4–E). These galls were elongate-clavoidal in shape and covered with a

whitish tomentum (Fig. 4B, C). They averaged 14.9 ± 0.6 (range, 6.0–41) mm in length and 4.8 ± 0.1 (range, 1.7–7.8) mm in widest width near the apices, expanding gradually distally from a basal, greenish, tomentose, side branch or stem, and incorporating an average of 3.9 ± 0.1 (range, 1–7) nodes. The galled branch or shoot tips were not shortened in length, but rather mainly expanded in width, and like their ungalled counterparts, bore no or from one to five vegetative or floral branches laterally and apically (Fig. 4). Some of these apical branches were killed when the bud caps were formed. The cavities within these mature galls measured 7.1 ± 0.3 (range, 3.1–18.9) mm long by 2.6 ± 0.1 (range, 1.3–6.9) mm in maximum width. Larger galls typically contained the most puparia, which lay freely, touching laterally or apically, within the common cavity (Fig. 4E).

Adult.—Adults emerged through the same exit tunnel after pushing aside the gall cap. Adults were long-lived under insectary conditions, as males averaged 48 ± 15 (range, 21–158) days, and 18 females (Fig. 4F) averaged 74 ± 11 (range, 31–172) days. A 7 week-old female contained 35 full-size ova, and eight 3–4 week-old females laid an average total of 24 ± 4 (range, 7–34) eggs in ovipositional cagings. No free-living adults were observed in nature.

In petri dish arenas, both sexes displayed synchronous and asynchronous supinations along with wing vibrations and hamation. During asynchronous supination, one wing was extended forward 90° to a point perpendicular to the body, and supinated to 90° with respect to the substrate. As the wing was extended it was vibrated in a plane parallel to the wing blade faster than was observed with other *Trupanea* spp. studied (Headrick and Goeden 1994). When the wing reached its maximum forward position, it was held for ca. 1 second, then returned to the resting position, flat upon the dorsum, and held still while the other wing was extended. Male courtship displays began in the mornings, usually after 0900 h PST and ended ca. midday. The courtship display was similar to that described for other species of *Trupanea* by Headrick and Goeden (1991, 1994) and Knio et al. (1996b). Males of *T. signata* regularly hung upside down from the covers of arenas when displaying and distending their abdomens. When the abdomen was distended, it was held flexed and synchronous or asynchronous wing displays were exhibited; however, when a female was near, males always reverted to synchronous wing extensions. Mating was not observed in this species, but see Headrick and Goeden (1994) for descriptions of mating behaviors common to several southern California species of *Trupanea.*

Seasonal history.—The life cycle of *T. signata* in southern California follows the aggregative pattern in which the long-lived adults in reproductive diapause overwinter probably in riparian habitats and aggregate on preblossom host plants during the following spring to mate and reproduce (Headrick and Goeden 1994). A second late-summer or early-fall generation reproduces on flowering shoots of *G. luteo-album,* and another generation or two may be produced on the above-mentioned, or as yet unidentified, alternate host plants, especially at higher elevations.

Natural enemies.—Two species of Hymenoptera were reared from puparia of *T. signata* as solitary, larval-pupal endoparasitoids: *Eurytoma* sp. (Eurytomidae) and *Pteromalus* sp. (Pteromalidae). Among 49 adult parasitoids recovered, nine (18%) were *Eurytoma* sp. and 40 (82%) were *Pteromalus* sp.

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